

*Sciurus niger*. By John L. Koprowski

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*Sciurus niger*

Fox Squirrel

- Sciurus niger* Linnaeus, 1758:64. Type locality probably southern South Carolina (Hall, 1981).  
*S. cinereus* Linnaeus, 1758:64. Type locality, "America Septentrionali."  
*S. vulpinus* Gmelin, 1788:147. Type locality, "eastern United States including Blue Mountains" of Pennsylvania.  
*S. capistratus* Bosc, 1802:145. Type locality from "Charleston, South Carolina."  
*S. rufiventer* Geoffroy St.-Hilaire, 1803:176. Type locality, Mississippi Valley probably between southern Illinois and central Tennessee (Osgood, 1907).  
*S. ludovicianus* Custis, 1806:47. Type locality, "Red River of Louisiana."  
*S. ruber* Rafinesque, 1820:4. Type locality "Missouri Territory."  
*S. macroura* Say, 1823:115. Type locality, "northeastern Kansas." (Not *Sciurus macrourus* Pennant, a species of *Ratufa*.)  
*S. magnicaudatus* Harlan, 1825:178. Renaming of *S. macroura*.  
*S. texianus* Bachman, 1839:86. Type locality, "Mexico."  
*S. subauratus* Bachman, 1839:87. Type locality, "procured in the markets of New Orleans."  
*S. auduboni* Bachman, 1839:97. Type locality unknown but probably near New Orleans, Louisiana.  
*S. rubricaudatus* Audubon and Bachman, 1851:30. Type locality, "Kentucky."  
*S. sayii* Audubon and Bachman, 1851:274. Type locality, somewhere in bottomlands of Wabash, Illinois, or Missouri rivers, or Michigan (Hall, 1981).  
*S. limitis* Baird, 1855:331. Type locality "on Devil's river, [Valverde Co.], Texas."  
*Macroxus neglectus* Gray, 1867:425. Type locality "Wilmington, Newcastle Co., Delaware."

**CONTEXT AND CONTENT.** Order Rodentia, Suborder Sciurognathi, Family Sciuridae, Subfamily Sciurinae, Tribe Sciurini, Subtribe Sciurina, Genus *Sciurus*, Subgenus *Sciurus*. Twenty-eight species of *Sciurus* are known (Hoffmann et al., 1993); 10 subspecies of *S. niger* are recognized (Hall, 1981):

- S. n. avicennia* Howell, 1919:37. Type locality "Everglade, Lee County, Florida."  
*S. n. bachmani* Lowery and Davis, 1942:156. Type locality "10 mi. NW Enon, Washington Parish, Louisiana."  
*S. n. cinereus* Linnaeus, 1758, see above. Type locality restricted to "Cambridge, Dorchester County, Maryland" by Barkalow (1956). (Includes *neglectus*.)  
*S. n. limitis* Baird, 1855, see above.  
*S. n. ludovicianus* Custis, 1806, see above. Type locality restricted to Natchitoches Parish by Lowery and Davis, 1942:164. (Includes *texianus*.)  
*S. n. niger* Linnaeus, 1758, see above. (Includes *capistratus*.)  
*S. n. rufiventer* Geoffroy St.-Hilaire, 1803, see above. (Includes *ruber*, *macroura*, *magnicaudatus*, *rubricaudatus*, *sayii*.)  
*S. n. shermani* Moore, 1956:56. Type locality from "2 miles E. of University of Florida Conservation Reserve, Welaka, Putnam County, Florida."  
*S. n. subauratus* Bachman, 1839, see above. Type locality restricted to Iberville Parish, Louisiana by Lowery and Davis, 1942:166. (Includes *auduboni*.)  
*S. n. vulpinus* Gmelin, 1788, see above.

**DIAGNOSIS.** *Sciurus niger* lacks an upper P3 unlike sympatric congeners, *S. aberti*, *S. carolinensis*, *S. griseus*, and exotic *S. aureogaster* in Florida. Where sympatric with *S. aberti*, *S. niger*

lacks hair tufts on the ears, dorsal pelage is not gray, baculum lacks a keel formed by an expanded distal end and is <16 mm long (Hall, 1981; McGrath 1987). *S. carolinensis*, the only congener with which geographic overlap is appreciable, is usually >20% smaller in body size, and guard hairs are tipped with white not tawny or orange (Flyger and Gates, 1982). However, *S. niger* from the eastern United States may have white-tipped guard hairs, but the larger body size of fox squirrels remains evident. Unlike *S. griseus*, introduced *S. niger* lacks a gray dorsum, the baculum lacks a distal keel and ventral tuberosity, and the posterior of the jugal is not twisted to reveal the medial surface (Hall, 1981; McGrath, 1987).

**GENERAL CHARACTERS.** *Sciurus niger* (Fig. 1) is a medium-sized tree squirrel with no sexual dimorphism in size or color. Ranges of external measurements (in mm) are: total length, 454-698; length of tail, 200-330; length of hind foot, 51-82 (Hall, 1981). Body mass ranges from 507-1,361 g (Flyger and Gates, 1982).

Dorsal pelage is variable; fox squirrels from the western and northern portions of the natural range are grizzled with a suffusion of buff to orange. The venter can be white to cinnamon but usually is rufous (Baumgartner, 1943a; Flyger and Gates, 1982). Fox squirrels in the southeastern United States are grizzled gray to agouti to black on the dorsum with white or cream nose, ears, and feet, and a black crown and nape (Kiltie, 1992; Moore, 1956; Weigl et al., 1989). Fox squirrels from the central United States coast are silvery gray and may be washed with buff on the hips, feet, and head; tail is pale gray; underparts are white to pale gray but may be cinnamon (Flyger and Gates, 1982). Melanism is common, especially in the southern United States (Kiltie, 1989, 1992). Albinism is rare (Baumgartner, 1943a; Moore, 1956).

The skull (Fig. 2) is short with broad, expanded zygomatics. The braincase is broad and posteriorly depressed. The rostrum is laterally compressed and narrow; the frontal area is flattened; auditory bullae are moderately inflated. Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20 (Flyger and Gates, 1982). Mean cranial measurements of 41 specimens from Arkansas, Florida, Kansas, Louisiana, Maryland, and Mexico (in mm) are: greatest length of skull, 66.2; zygomatic breadth, 37.8; palatal length, 29.9; diastema length, 16.0; least interorbital breadth, 20.3; nasal length, 24.2; length of maxillary toothrow, 12.0 (McGrath, 1987).

**DISTRIBUTION.** *Sciurus niger* is found in much of the eastern and central United States extending northward into the



FIG. 1. *Sciurus niger* from Eugene, Lane Co., Oregon.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Sciurus niger* (female from near Lindsborg, McPherson Co., Kansas, University of Kansas Museum of Natural History 16250). Greatest length of cranium is 62.9 mm. Photographs by S. Hagen.

southern prairie provinces of Canada (Fig. 3). The western periphery of the range is expanding along narrow riverine corridors (Adam, 1984; Knapp and Swenson, 1986). Introductions occurred in California, Colorado, Idaho, New Mexico, North Dakota, Oregon, Texas, and Washington in the United States and Ontario in Canada (Flyger and Gates, 1982).

**FOSSIL RECORD.** Fossils of the earliest *Sciurus* from the Miocene in Europe and North America are indistinguishable from the present day genus (Emry and Thorington, 1984). *S. niger* is reported from nine late Rancholabrean faunas (Kurtén and Anderson, 1980); the species was a late immigrant into Florida (Devil's Den: Martin and Webb, 1974).

**FORM AND FUNCTION.** Although early researchers believed there was only one annual molt (Moore, 1957), two molts likely occur. The spring molt begins in March and proceeds posteriorly from the head; the autumn molt begins in September and progresses anteriorly from the flanks. The annual tail molt begins

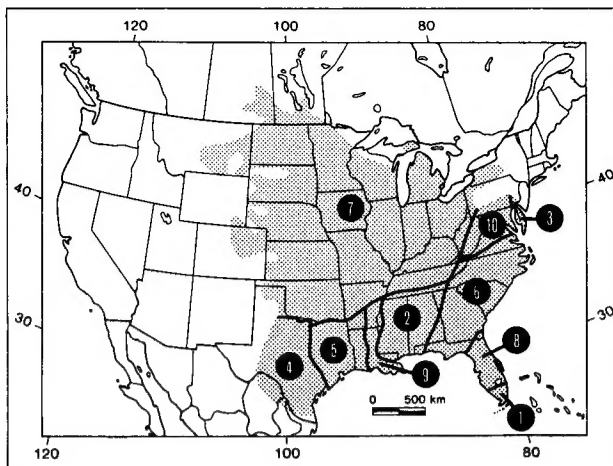


FIG. 3. Distribution of *Sciurus niger* in North America; 1, *S. n. avicennia*; 2, *S. n. bachmani*; 3, *S. n. cinereus*; 4, *S. n. limitis*; 5, *S. n. ludovicianus*; 6, *S. n. niger*; 7, *S. n. rufiventris*; 8, *S. n. shermani*; 9, *S. n. subauratus*; 10, *S. n. vulpinus* (modified from Hall, 1981).

in July or August (Flyger and Gates, 1982). Lactating females molt after young are weaned (Baumgartner, 1943a). The molt into adult pelage occurs at 75–90 days of age (Moore, 1957). During winter, ears are heavily furred with pale colored hair (Flyger and Gates, 1982); the foot sole becomes densely haired (Pocock, 1923). Mystacial vibrissae are longer after allowing for body size than those of ground-dwelling sciurids (1.71:1 ratio of vibrissal length : head width; Ahl, 1987).

The eight mammae (four pectoral, two abdominal, two inguinal) become black in the first pregnancy and generally retain this coloration (Flyger and Gates, 1982). Ten mammae were reported (Svihla, 1931).

Incisor growth is indeterminant; molariform cheekteeth exhibit brachyodont and bunodont structure (Flyger and Gates, 1982). Upper incisors are opisthodont; the mean inciso-rostral angle is 76.1° with incisors covering an arc of 208° (Landry, 1957).

The stance is plantigrade (Gurnell, 1987). Anatomical adaptations for climbing and jumping include: sharp recurved claws, elongated digits and limbs, well-developed extensors of digits and flexors of forearms, trapezius group muscles, clavicles, and abdominal musculature. The first digit is reduced on the front feet. In Kansas specimens, the average lengths of the other digits (in mm) are: 35, 40, 43, 35; carpals are pisiform and average 4 mm. There are an average of 26 caudal, 3 (or 4) sacral, 7 lumbar, 12 thoracic vertebrae, and 12 thoracic ribs (Peterka, 1936). An adult female with a fifth leg attached by soft tissue at the inguinal area has been described (Bowers and Kirkland, 1968).

Clinal variation in reverse of Bergmann's Rule exists in body size east of the Appalachians; body size is smallest in the north. Fox squirrels to the west follow the pattern predicted by Bergmann's Rule (Weigl et al., 1989). An east–west cline also exists, with the smallest fox squirrels in the west (Purdue, 1980).

Heart rate ranges from 150 to 450 beats/min; fear tachycardia occurs in free-ranging animals in response to stimuli (Smith and Johnson, 1984). Mean hematological characteristics are: hematocrit = 38%, red blood cell count =  $7.33 \times 10^6$  cells/mm<sup>3</sup>, and mean corpuscular volumes = 52  $\mu\text{m}^3$  (Dunaway and Lewis, 1965). Mean rectal temperature is 40.6°C (Havera, 1979a). The tail possesses a counter-current system of vascular bundles at the base; the tail's insulative value increases 17.8% to 0.034°C kcal<sup>-1</sup>h<sup>-1</sup>m<sup>-2</sup> when the tail is raised above the body while providing shade and slowing heat gain (Muchlinski and Shump, 1979).

Energy assimilation rates range from 388 to 578 kJ/squirrel/day. Food consumption peaks in spring or autumn with a voluntary decrease in winter (Knee, 1983). Fox squirrels fed lab show consumed 49.3 g/day in May, 46.1 g/day in October, and only 18.3 g/day in February (Havera, 1989b). Juveniles consume 50% more food per unit of metabolic weight (body mass<sup>-0.75</sup>) than adults (Short and Duke, 1971). Energy requirements for maintenance in autumn

are 162 kcal day<sup>-1</sup> kg<sup>-0.75</sup> (Husband, 1976). Urinary loss of energy is 0.6–8.7% and digestive efficiencies range from 80% on a lab chow diet to 96% on a black walnut (*Juglans nigra*) diet; body mass follows food consumption trends with peaks in winter and lows in summer with a peak-to-trough difference of about 10% (Knee, 1983).

Retinal photoreceptors have separate functions permitting photopic and scotopic vision. Under conditions of dark adaptation, the absorption peak is 500 nm, but the distribution under light adaptation is bimodal with peaks at 460 and 560 nm. Color vision is probably dichromatic or possibly trichromatic with peak activity at 450 and 540 nm (Jacobs, 1974). Visual acuity measured by detection of oscilloscope square waves increased from 2.8 cycles/degree at a distance of 30 cm in low light to 3.9 cycles/degree in bright light (Jacobs et al., 1982).

The brain averages 9.3 g (Meier, 1983). Adult carcasses from Illinois during autumn and spring (Havera, 1977) are composed of 6.9% fat, 67.6% water, 12.5% ash, and 4,829 cal/g; mean kidney fat index was 32.7; mean percent liver fat was 10.43. Adrenal glands of females average 149.5 µg; male glands are significantly smaller at 116.6 µg (Havera, 1977). Mean organ weights (in g) are: kidneys = 1.98, pancreas = 1.82, lungs = 8.75, liver = 18.31, and heart = 3.96. Kidney fat index is highly correlated with carcass fat; fat levels are 4.5–8.5% and kidney fat indices are 15–40. Pregnant females have more carcass fat on average (8.4%) than other females (6.2%); fat levels fall to 6.1% during lactation and 4.7% after lactation. Animals that die from shock have low carcass fat, liver fat, and kidney fat indices (Havera, 1977).

Techniques for aging animals in the field (juvenile <6 months, subadult 6–12 months, adult >1.0 year) are most accurate in fall when age class differences are most obvious, but may overestimate age during years of precocious reproduction (McCloskey, 1977). Condition and coloration of the scrotum (posterior scrotum bare and black in adults but partially haired and gray to brown in subadults) and mammae (enlarged and black-tipped in adults) as well as tail pelage molt and pigmentation patterns indicate age class (Larson and Taber, 1980). Laboratory methods include eye-lens weight for ages <2.5 year (in October: adults, >40 mg, spring-born, 29–39 mg, summer born, <29 mg; Beale, 1962) and timing of epiphyseal closure (adult females fuse by 50 weeks, adult males fuse near 54 weeks; Carson, 1961). Tail pelage and scrotum and nipple coloration are highly correlated with age (McCloskey, 1977).

**ONTOGENY AND REPRODUCTION.** Females may bear young at 8 months of age (McCloskey and Vohs, 1971), but most do not reproduce until >1.25 years of age (Harnishfeger et al., 1978); reproductive longevity of females may be >12.0 years (Koprowski et al., 1988). Only 2 of 59 squirrels <1 year old but >50% of females 2–4 years old reproduced in Illinois (Harnishfeger et al., 1978). The vagina is closed in anestrous and prepubescent females; an enlarged pink vulva indicates estrus (Brown and Yeager, 1945). Although fox squirrels may mate at any time in the year, most breeding is in November–February with a December peak and April–July with a June peak (Brown and Yeager, 1945; Moore, 1957). Summer breeding may not occur (McCloskey and Vohs, 1971; Weigl et al., 1989). Gestation is 44 or 45 days (Flyger and Gates, 1982).

Prior to estrus, males follow females and smell the perineal region. During the rut, home ranges of males in Illinois increase from 1.2 ha for non-mating males to 1.9 ha for breeding males (Benson, 1980). Males aggregate in the home range of a female on the morning she begins her 1 day estrus (Koprowski, 1993a). A linear dominance hierarchy forms among males; females mate with several males. After a dorsal mount, copulation lasts <30 sec with locking, thrusting, and multiple intromissions (Koprowski, 1993a; McCloskey and Shaw, 1977). An acellular copulatory plug forms in the vagina from the coagulation of male semen (Koprowski, 1992).

The os clitoridis is 2.9–4.0 mm long (Layne, 1954; Long and Frank, 1968). Ovarian follicular diameters are largest (847.2 µm) in pregnancy and smallest in nonreproductive females (17.8 µm); corpora lutea atrophy after pregnancy. Preimplantation loss was 12.5% (Havera et al., 1985). Production of litters follows the bimodal distribution of breeding (Brown and Yeager, 1945). Average litter sizes range from 1.97 to 3.35 throughout the species range; the mode is 2 or 3 (Harnishfeger et al., 1978; McCloskey and Vohs, 1971). Seven fetuses have been reported (Hoover, 1954). Female reproductive levels are extremely variable between seasons and years (Harnishfeger et al., 1978; Weigl et al., 1989). In Illinois, the 8-year

average for spring breeding was 30%; summer average was 11% (Harnishfeger et al., 1978). None to >90% of adults reproduce each year (Harnishfeger et al., 1978; Weigl et al., 1989). Only 2% of females produced 2 litters/year (Harnishfeger et al., 1978) but this percentage may be higher in some populations (Allen, 1942). Reproduction may be tightly linked with food availability (Nixon and McClain, 1969). Prevalence of lactation fell from 88 to 0% after a poor food crop (Weigl et al., 1989).

The baculum is 12.4 mm long in *S. n. rufiventer* and 13.3 mm long in *S. n. niger* (Long and Frank, 1968; Wade and Gilbert, 1942). Males reach sexual maturity as early as 10–11 months (Kirkpatrick, 1955) and undergo an irregular cycle of testicular development; functional testes are pendant in the scrotum. Two annual peaks in male reproductive activity occur in November–February and May–July; however, functional males are found in all months (Brown and Yeager, 1945; Kirkpatrick, 1955; Weigl et al., 1989). A period of male sexual quiescence characterized by regressed testes, degenerated glands, and apparent cessation of spermatogenesis usually occurs August–October (Kirkpatrick, 1955; Mossman et al., 1955). Active testes averaged 6.9 g, but inactive testes were 0.4 g (Kirkpatrick, 1955). The prostate gland is an elongated ovoid, Cowper's glands are paired and spherical, seminal vesicles are paired and prismatic in shape, and the single bulbar gland is three-lobed and conical in shape (Kirkpatrick, 1955; Mossman et al., 1955). Epididymal spermatozoa aggregate into cylindrical bodies then separate becoming single or a rouleaux (Martan et al., 1970).

Neonates are naked except for vibrissae, weigh 13–18 g, and are 50–60 mm long. Claws are well developed. The dorsum darkens after 7–10 days as hair emerges. By 3 weeks of age, downy hair begins to fill the dorsum of the tail, the ears open, and the lower incisors erupt. Eyes open, upper incisors erupt, and hair appears on the ventral tail surface in week 5. Weaning begins at 8 weeks and is not complete until as late as 12 weeks of age (Allen, 1942). The instantaneous positive growth rate is highest during the first week of life (87% of birth mass) and gradually declines to 8% at weaning; body mass at 1 year of age averages 92% of maximum body mass (Nixon et al., 1991).

**ECOLOGY.** Although found in a diversity of deciduous and mixed-forest habitats, fox squirrels are common in forest patches <40 ha with an open understory (Nixon and Hansen, 1987). Low understory stem densities are an important component in some localities (Taylor, 1974) but not in others (Brown and Batzli, 1984). Densities of *S. niger* are highest in habitats composed of trees that produce winter-storable food such as oaks (*Quercus*), hickories (*Carya*), walnuts (*Juglans*), and pines (*Pinus*; Nixon and Hansen, 1987; Weigl et al., 1989). Due to annual variability in mast production, a diversity of tree species is important to support high densities of fox squirrels (Nixon and Hansen, 1987).

Western range extensions are associated with riverine corridors of cottonwoods (*Populus deltoides*; Knapp and Swenson, 1986) and fencerows of osage orange (*Maclura pomifera*; Packard, 1956). In Colorado, fox squirrels inhabit mixed conifer-deciduous forests (Littlefield, 1984). In Florida, *S. n. avicennia* is restricted to diminishing stands of cypress (*Taxodium distichum*), slash pine (*Pinus elliotii*) savanna, and mangrove (*Avicennia germinans*) swamps (Williams and Humphrey, 1979). Populations of *S. n. limitis* and *S. n. ludovicianus* in Texas are found primarily in upland pine-oak-hickory woodlands (Goodrum, 1937; Lowery and Davis, 1942). Endangered *S. n. cinereus* is found in savanna of mature hardwoods and loblolly pine (*P. taeda*; Taylor, 1974). In North Carolina, *S. n. niger* frequents open mature pine-oak, especially longleaf pine (*P. palustris*) and turkey oak (*Q. laevis*; Weigl et al., 1989). *S. n. shermani* in Florida prefers longleaf pine savanna and edges of live oak forests (*Q. virginiana*; Kantola and Humphrey, 1990). The rapid loss of preferred habitats is likely responsible for the precarious conservation status of four subspecies: *S. n. avicennia*, *S. n. cinereus*, *S. n. niger*, *S. n. shermani*.

Formation of den cavities requires 8–30 years depending on wood type (Baumgartner, 1939a). Addition of artificial nest boxes did not increase densities or survival except for adult males (Nixon et al., 1984). However, 1–2 boxes/2.5 ha may be beneficial (Nixon and Hansen, 1987). Girdling or otherwise deadening of hardwoods and prescribed burning are detrimental to squirrels (Hedrick, 1973). Selective cutting of trees ≥30.5 cm without removal of culled trees has little effect on population parameters except for temporarily low recovery rates of females after >40% of the merchantable volume



was removed (Nixon et al., 1980). Winter feeding with corn did not increase survival or densities (Havera and Nixon, 1980).

Densities of fox squirrels in woodlots in the midwestern United States are 1.0–3.5/ha (Baumgartner, 1943b; Nixon and Hansen, 1987) but reach 12 squirrels/ha (Koprowski, 1985). However, densities in the southeastern United States are 0.12 squirrels/ha (Kantola and Humphrey, 1990) and 0.04 squirrels/ha (Moore, 1957) for *S. n. shermani* and 0.05 squirrels/ha for *S. n. niger* (Weigl et al., 1989). Food can be limiting during winter when autumn nut crops may be exhausted prior to spring flowering of trees and late spring-early summer when fruits may be depleted prior to ripening of nut crops. After frost damages developing tree seeds, body mass, survival, and reproduction decrease (Koprowski, 1991a; Nixon and McClain, 1969).

Sex ratios (male:female) vary from 0.88–1.05:1 in nestlings (Brown and Yeager, 1945; Weigl et al., 1989), 0.82–1.13:1 in juveniles, and 1.10–1.14:1 in adults (Nixon et al., 1975; Weigl et al., 1989) but do not differ from a 1:1 sex ratio. Annual trends in age structure reflect seasonal reproduction with adults composing 83% of the population in April prior to emergence of spring litters and only 30% in October when juveniles from both spring and summer litters remain in the population (Brown and Yeager, 1945). A declining population consisted of a few old adults (Nixon and McClain, 1969). Immature animals compose 13–81% of populations (Brown and Yeager, 1945; Nixon et al., 1975).

Durations of residence were 4.7 months for juveniles, 13.5 months for subadults, 27.4 months for yearlings, and 25.7 months for adults; no sex differences were evidenced (Hansen et al., 1986). Annual adult survivorship is generally >60% with mean annual mortality estimated as 34% for males and 37% for females (Hansen et al., 1986). Dispersal peaks in autumn when most subadults move; however, this autumn-shuffling may include many adults (Allen, 1943; Baumgartner, 1943b; Koprowski, 1985). Mass migrations are rare, but small scale migrations are observed occasionally (Schorger, 1949). Turnover times (99.1% of the population) were 11.7 years for unhunted populations (Hansen et al., 1986) but <3.5 years for hunted populations. Populations can sustain a hunting loss of <40%, but only immigration sustained a population with an 80% loss (Nixon et al., 1974, 1975). Maximum longevity is 12.6 years for females and 8.3 years for males (Koprowski et al., 1988); a captive female survived 13 years (Flyger and Gates, 1982). Weather and survival are not correlated (Hansen et al., 1986). Only extremes in seed crops likely affect adult survival (Hansen et al., 1986; Nixon and McClain, 1969; Nixon et al., 1975), although juvenile survival is influenced particularly by seed crops (Koprowski, 1991a). Supplemental feeding with corn did not increase survival (Havera and Nixon, 1980); however, supplements of natural mast may increase survival and reproduction (Brown and Batzli, 1985a).

Predators of fox squirrels include timber rattlesnakes (*Crotalus horridus*), black rat (*Elaphe obsoleta*) and pine (*Pituophis melanoleucus*) snakes, goshawks (*Accipiter gentilis*), red-tailed (*Buteo jamaicensis*), red-shouldered (*B. lineatus*), rough-legged (*B. lagopus*), ferruginous rough-legged (*B. regalis*) hawks, and great horned owls (*Bubo virginianus*). Mammalian predators include opossums (*Didelphis virginiana*), weasels (*Mustela frenata*), raccoons (*Procyon lotor*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), bobcats (*Felis rufus*), wolves (*Canis lupus*), coyotes (*C. latrans*), dogs, and cats (Flyger and Gates, 1982; Packard, 1956; Weigl et al., 1989).

Pesticide levels in tissues are low; however 11% of assayed squirrels from Illinois contained dieldrin (mean = 0.0011 ppm) and 89% contained DDE (mean = 0.0041 ppm; Havera and Duzan, 1977). Normal porphyria characterizes fox squirrels and resembles congenital erythropoietic porphyria in humans. Porphyrin metabolism is defective and uroporphyrin I accumulates in teeth, bones, and tissues. As a result, bones are pink; bones, thin spleen tissue sections, and urine fluoresce bright red under ultraviolet light. Fox squirrels do not display skin lesions or hemolytic anemia and can serve as a useful model for medical research (Flyger and Levin, 1977). California encephalitis virus and western equine virus are known from fox squirrels (Flyger and Gates, 1982). Rabies is rare (Capucci et al., 1972). *Francisella tularensis* (tularemia), *Yersinia pestis* (plague) in Colorado, and *Leptospira grippotyphosa* (leptospirosis) in Florida have been reported (Flyger and Gates, 1982). Coccidiosis-related deaths were reported in Iowa (McCloskey and Vohs, 1971).

Larvae of bot flies (*Cuterebra emascuator*) parasitize squirrels

in autumn when the subcutaneous myiasis infest 5% of animals in Mississippi (Jacobson et al., 1979, 1981). Infestations of mange mites (*Notodres*, *Sarcoptes*, and *Cnemidoptes*) may result in death (Kazacos et al., 1983; Flyger and Gates, 1982). Flyger and Gates (1982) provide an extensive list of parasites from which the following list was compiled unless otherwise noted. Protozoa—*Eimeria ascotensis*, *E. confusa* (Joseph, 1975), *E. kniplingi*, *E. lancasterensis*, *E. ontarioensis* (Joseph, 1975); Cestoda—*Bothriocephalus sciuri*, *Choanotaenia sciuricola*, *Citellinema bifurcatum*, *Cysticercus passeriformes*, *Hymenolepis diminuta*, *Mesocostoides latus*, *Multiceps serialis*, *Raillietina bakeri*, *Taenia hydatigena*, *T. mustelae* (Langham et al., 1990), *T. pisiformis*, *T. taeniaeformis*; Acanthocephala—*Moniliformis clarkii*; Nematoda—*Ascaris columbianus*, *A. lumbricoides*, *Bohmiella wilsoni*, *Capillaria hepatica*, *Enterobius sciuri*, *Heligmodendrium hassalli*, *Macracanthorhynchus hirudinaceus*, *Physaloptera massino*, *Strongyloides robustus*, *Trichinella spiralis*; Acarina—*Amblyoma americanum*, *A. maculatum*, *A. tuberculatum*, *Atricholaelaps glasgowi*, *A. megaventralis*, *Dermacentor variabilis*, *Eulaelaps stabularis* (Moore, 1957), *Eutrombicula alfreddugesi*, *Haemaphysalis leporispalustris*, *Haemolaelaps megaventralis*, *Ixodes cookei*, *I. hearlei*, *I. scapularis* (Moore, 1957), *Notodres douglasi* (Kazacos et al., 1983), *Sarcoptes scabiei*, *Trombicula alfreddugesi* (Moore, 1957), *T. whartoni* (Moore, 1957); Anoplura—*Enderleinellus longiceps*, *Hoplopleura sciuricola*, *Neohaematopinus sciurinus*; Siphonaptera—*Ceratophyllus fasciatus*, *Ctenocephalides felis*, *Echidnophaga gallinacea*, *Hoplopsyllus offinis*, *Leptopsylla segnis*, *Opisodasys robustus*, *Orchopeas howardi*; Diptera—*Cuterebra emascuator*.

Fox squirrels use ≤9 nests annually (Nixon and Hansen, 1987). Leaf nests (or drays) average 34 cm in diameter and are constructed of a platform of twigs placed on tree limbs, a shell of twigs and leaves, and usually a lining of shredded and woven material. Summer leaf nests are not built as sturdily and may consist only of a platform (Baumgartner, 1943b; Stoddard, 1919). Cavities within trees are also used (Baumgartner, 1939a) as well as tree stumps and burrows of other animals (Moore, 1957). Den cavities and nest boxes are used most frequently in winter (Christisen, 1985) with leaf nests most commonly occupied in warmer months (Geeslin, 1970). Occupied nest boxes in winter were 25.9°C warmer than ambient temperatures (−21 to 34°C) and averaged 31°C warmer than empty boxes (Havera, 1979a). Entrance openings to nest cavities average 7.4 by 9.4 cm in size (Baumgartner, 1939a). Squirrels extensively use and may rear young in drays (Kantola and Humphrey, 1990; Stoddard, 1919).

Eastern gray squirrels and fox squirrels can be syntopic (Armitage and Harris, 1982). Food preferences are similar (Smith and Follmer, 1972). *S. niger* females displace *S. carolinensis* from concentrated food sources in the breeding season, but eastern gray squirrel females are more efficient at finding food (Brown and Batzli, 1985b). Removal of adult female fox squirrels led to slight shifts in space use of female eastern gray squirrels (Brown and Batzli, 1985a). Eastern gray squirrels replaced fox squirrels in a suburban neighborhood as food trees matured (Sexton, 1990). Eastern gray squirrels inhabit areas with dense understory (Nixon and Hansen, 1987). Woodlot size may be important; larger woodlots tend to have higher densities of understory and eastern gray squirrels (Brown and Batzli, 1984). Little ecological overlap occurs between *S. niger* and *S. aberti* in Colorado (Littlefield, 1984).

Fox squirrels feed heavily on tree seeds during much of the year. Tree buds and flowers are used primarily in winter and spring. In spring and early summer fruits and seeds of a limited number of species such as mulberry (*Morus*), hawthorn (*Crataegus*), and maples (*Acer*) are eaten until nuts ripen (Koprowski, 1991a; Reichard, 1976). Although fox squirrels in Missouri fed on 109 plant items, only 18 items accounted for 82% of the total volume; 60% of the stomachs analyzed contained only one food item (Korschgen, 1981). Fox squirrels feed heavily on the nuts, flowers, and buds of ≥21 species of oak, 8 species of hickory and pecan (*Carya*), walnuts, beech (*Fagus grandifolia*), and longleaf pine when available (Korschgen, 1981; Nixon et al., 1968; Weigl et al., 1989). Other important foods (Baumgartner, 1939b; Boulware, 1941; Bugbee and Riegel, 1945; Korschgen, 1981; Nixon et al., 1968; Packard, 1956; Weigl et al., 1989) include the fruits, seeds, buds, or flowers of ash (*Fraxinus*), maples, mulberry, osage orange, hackberry (*Celtis*), elms (*Ulmus*), buckeye (*Aesculus*), wild cherries (*Prunus*), chinquapin (*Castanea pumila*), dogwoods (*Cornus*), hawthorn, black gum (*Nyssa sylvatica*), sweet gum (*Liquidambar styraciflua*), hazelnut (*Cor-*

*ylus americana*), pawpaw (*Asimina triloba*), persimmon (*Diospyros*), blue gum (*Eucalyptus globulus*), Russian olive (*Elaeagnus angustifolia*), Kentucky coffee tree (*Gymnocladus dioica*), honey locust (*Gleditsia triacanthos*), tulip tree (*Liriodendron tulipifera*), hop hornbeam (*Ostrya virginiana*), cottonwood, and willow (*Salix*). Seeds and catkins of gymnosperms are also eaten, including cedar (*Juniperus*), cypress (*Taxodium distichum*), and pines (especially longleaf pine and pond pine, *P. serotina*, in the southeastern United States; Packard, 1956; Weigl et al., 1989). Herbaceous species eaten include grasses, sedges, grape (*Vitis*), cocklebur (*Xanthium*), greenbrier (*Smilax*), huckleberry (*Gaylussacia*), blueberry (*Vaccinium*), bittersweet (*Celastrus scandens*), and blackberry (*Rubus*; Baumgartner, 1939b; Korschgen, 1981; Nixon et al., 1968). The sugary pith of yellow buckeye (*A. octandra*) is eaten (Havera et al., 1976) and bark is occasionally ingested (Packard, 1956). Corn, oats, sorghum, soybeans, and wheat are eaten especially in winter; fruits of apple, cherry, blueberries, and oranges are also eaten (Baumgartner, 1939b; Korschgen, 1981; Wolf and Roest, 1971). Gravel and soil are ingested by females in winter and spring; fungi are consumed primarily in summer and winter (Korschgen, 1981; Weigl et al., 1989). A preference for salt (primarily sodium) occurs in spring as potassium uptake rises and again in autumn in association with low salt concentrations of nuts (Weeks and Kirkpatrick, 1978).

Animal foods are usually ingested in trace amounts including gall insects (*Pemphigus*, sp., *Pachysylla mamma*), various species of moths, butterflies and caterpillars (Lepidoptera), grasshoppers (Acrididae), walkingsticks (Phasmidae), may-beetles (Scarabaeidae), cicadas (Cicadidae), weevils (Curculionidae), ants (Formicidae), and flies (Diptera; Baumgartner, 1939b; Bugbee and Riegel, 1945; Korschgen, 1981). Other animal foods include birds and bird eggs (Packard, 1956; Shaffer and Baker, 1991) and dead fish (Fairbanks and Koprowski, 1992). Cannibalism has been reported (Allen, 1943).

Damage by fox squirrels is considered a problem only on a local scale (Gurnell, 1987). Historically, corn crops of Native Americans and early colonists suffered high depredation (Schorger, 1949). Pecans, English walnuts, avocados, oranges, and strawberries are eaten but losses are not excessive (Flyger and Gates, 1982; Wolf and Roest, 1971). The oak wilt fungus is transmitted by fox squirrels under experimental conditions (Himelick and Curl, 1955). Fox squirrels can be a nuisance by raiding gardens and bird feeders. Live-trapping with release of squirrels >10 km away may effectively deal with problem individuals (Flyger and Gates, 1982). State or provincial wildlife agencies must be contacted prior to trapping this game animal. Fox squirrels may be repelled from holes in wooden walls and roof shingles by using paradichlorobenzene or naphthalene (moth balls or crystals). Gnawing of plant stems or tree bark may be reduced with the application of tetramethylthiuram disulfide. Methyl nonyl ketone crystals and paradichlorobenzene are used to repel animals from garden and property borders, but effectiveness is questionable (Jackson, 1983). Fox squirrel use of electrical power equipment as pathways can result in power outages (Hamilton et al., 1989).

Economic value is primarily from hunting and travel-related revenues. Historically, squirrels were a quality food to Native Americans and the early European colonists (Schorger, 1949). The non-consumptive value of tree squirrels is also great; collectively, squirrels rank second to songbirds in value to nature watchers and photographers (Shaw and Mangun, 1984). Additionally, fox squirrels are excellent subjects for education on various problems in behavior and ecology (Brown and Downhower, 1987). By burying forest nuts in open grasslands, fox squirrels are instrumental in succession of grasslands to forests (Stapanian and Smith, 1986).

Fox squirrels can be live-trapped with box traps baited with peanuts, peanut butter, corn, sunflower seeds, or nuts and placed near large trees; prebaiting for several days may increase trap success (Baumgartner, 1940; Brown and Batzli, 1985a). Traps should be checked twice daily to prevent mortality. Success is greatest in winter and spring (Koprowski, 1985). Squirrels are safely handled in a wire mesh or cloth handling cone to restrict movement (Baumgartner, 1940; Weigl et al., 1989). Squirrels are temporarily marked for observation with fur dyes (Bernard, 1972). Semi-permanent identification is accomplished with ear tags (Baumgartner, 1940), or, if field observations are desired, by ear tags equipped with streamers (Koprowski et al., 1988). Permanent identification is possible by toe-clipping (Baumgartner, 1940) or, if field observations are desired, by freeze branding (Hadow, 1972) or freeze marking (Koprowski, 1991a). Time-area counts may be useful to estimate squirrel abundance but are labor-intensive and must be conducted during peak

periods of activity (Bouffard, 1982). Some mark-recapture methods especially in high density populations of trappable squirrels are useful in estimating abundance (Hansen et al., 1986; Koprowski, 1985; Nixon et al., 1984). Fox squirrels in the southeastern United States are difficult to trap; checking nest boxes at night is the most successful method of capture (Weigl et al., 1989).

Fox squirrel nestlings can be raised on milk followed by bread and milk and finally soft fruits and vegetables as young mature (Crandall, 1964). Adults can be maintained on a diet composed of a variety of nuts, seeds, fruit, lab chow, and a vitamin supplement; large (>2 by 2 by 4 m) outdoor pens with nest boxes are most successful (Weigl et al., 1989).

**BEHAVIOR.** Diel activity is bimodal in spring-fall peaking at 2 h after sunrise and 2–4 h before sunset; a unimodal pattern occurs in winter with a midday peak at 1000–1400 h (Adams, 1984; Geeslin, 1970; Hicks, 1949; Hilliard, 1979). In summer, an additional peak in activity may also occur from 1100–1200 h (Hicks, 1949). Greatest activity in winter is during early morning, possibly related to breeding activity (Packard, 1956). Activity is diurnal but may begin just before sunrise or continue shortly after sunset (Geeslin, 1970). Weather has a nebulous impact on activity; however, high winds (>14.5 km/h) result in low activity (Hicks, 1949). McCloskey (1975) details the ontogeny of behavior from birth to adulthood. Sleeping and crawling dominate the repertoire of nestlings until 21 days of age when they begin to walk. At day 33, nestlings groom and move their tails. Juveniles can run and jump at 37 days of age. Independent feeding and drinking begin about day 45 and caching was first observed at day 65.

Average home ranges vary from 0.85 to 17.2 ha for females and from 1.54 to 42.8 ha for males; the largest home ranges are reported in the southeastern United States (Adams, 1976; Benson, 1980; Geeslin, 1970; Hilliard, 1979; Kantola and Humphrey, 1990; Weigl et al., 1989). Home range overlap is extensive and territoriality is not evidenced (Allen, 1943; Benson, 1980). Adults, especially females, may defend exclusive core areas thereby limiting immigration (Havera and Nixon, 1978; Kantola and Humphrey, 1990).

Adult females are important in regulating densities. Ingress of juveniles and subadults of both sexes and adult females was higher on grids from which adult females were removed than on control grids or grids from which males were removed (Hansen et al., 1986). Furthermore, immigrant survival is negatively correlated with the number of resident adults, especially adult females (Hansen et al., 1986).

All juveniles probably disperse from their natal areas (Hansen et al., 1986; Koprowski, 1991b) although some may nest with their mother through a winter (Adams, 1984; Allen, 1943). Agonistic interactions peak during periods of heightened reproductive activity (Benson, 1980) and maternal aggression may be instrumental in natal dispersal (Adams, 1984). The longest dispersal movement reported is 64.4 km (Allen, 1943).

Sex and age are the primary determinants of dominance; males dominate females and adults dominate juveniles (Benson, 1980; Bernard, 1972). Threat is characterized by an upright stance with tail over the back and may be preceded or followed by a tail flick and rapid approach by the aggressor. Submissive animals usually retreat (McCloskey, 1975). Gregarious nesting is rare with <5% of nests occupied by >1 squirrel (Christisen, 1985; Koprowski, 1991b). Adult male groups during winter and adult male-female pairs during breeding seasons are the most common associations (Adams, 1984; Koprowski, 1991b; Nixon et al., 1984; Weigl et al., 1989). Juveniles and adult males aggregate more than adult females when outside of dens (Armitage and Harris, 1982).

Tail movements such as rapid fore-and-aft jerking are used to reduce aggression or signal an aggressor's intentions. The variable response of fox squirrels to tail movements suggests that more subtle visual signals are used (McCloskey, 1975; McCloskey and Shaw, 1977).

Traditional scent marking points are found in protected sites on trees and are visited regularly by male fox squirrels (Koprowski, 1993b), which deposit scent from glands in the oral-labial region (Benson, 1980). Females visit these points but rarely mark (Koprowski, 1993b). Both sexes mark substrate at non-traditional, dispersed sites while traversing their home ranges; dominant animals mark most often (Benson, 1980).

The most common vocalization by fox squirrels is a series of barks. A chatter bark is given after being startled. Tooth chatters

and breathy barks are indicative of restlessness and mild stress. Low frequency groans are emitted by restrained squirrels. Grunts and longer-lasting squeals are given by restrained animals and during male-male chases. A scream consisting of two parts is produced by distressed squirrels. A high pitched whine is given during mating chases (Zelley, 1971).

Fox squirrels swim by a dog-paddle with head, dorsum, and tail above the surface (Applegate and McCord, 1974). Squirrels can run 24.2 km/h at a gallop (Moore, 1957). Most feeding is accomplished in a bipedal stance with items manipulated in the forepaws. Vigilance is accomplished by a bipedal stance with varying degrees of erectness. Fox squirrels are adept climbers and frequently hang by the hindlimbs and forage with the forelimbs when feeding among tree limbs; climbing is accomplished in a trot or gallop.

Fox squirrels are classic scatterhoarders that disperse food caches. Nuts are carried in the jaws, a hole is dug with the forepaws, and the nut is buried below (<2 cm) the soil surface or covered with leaf litter (Cahalane, 1942). Between 33% and 99% of cached seeds are recovered (Cahalane, 1942; Stapanian and Smith, 1984). Olfaction is likely important in locating buried nuts. Accuracy in locating buried nuts decreases in dry, sandy substrates, possibly due to poor diffusion of chemical cues (Cahalane, 1942). Acorns with high lipid content are preferred, especially white oaks (Smith and Follmer, 1972). Red oak and black oak acorns were preferred over white oak acorns with a demonstrated preference for acorns of low tannin content (Ofcarcik et al., 1973); however, diets consisting solely of red oak or black oak acorns were the only nut diets to lead to loss of body mass (Baumgras, 1944; Havera and Smith, 1979). Food choices suggest squirrels forage to maximize energy gain (Smith and Follmer, 1972). Survival of buried nuts decreases with increased food content of the nut and density of nuts in the patch (Stapanian and Smith, 1984). Fox squirrels scatter caches in mutually exclusive areas at densities that minimize loss rates to seed competitors (Stapanian and Smith, 1978). Foraging strategies of free-ranging fox squirrels are complex and change between sites; patch choice is related to the highest short- and long-term rates of energy gain (Steele and Weigl, 1992).

**GENETICS.** The diploid number of chromosomes for *S. n. rufiventer* is 40; the fundamental number is 76. The X chromosome is a submetacentric and the Y chromosome is an acrocentric; autosomes consist of 14 metacentrics and 24 submetacentrics (Nadler and Sutton, 1967). Electrophoretic variation was detected at 18 of the 35 loci assayed including acid phosphatase, adenosine deaminase, creatine kinase, fumarase, glucose-6-phosphate dehydrogenase, isocitrate dehydrogenase, malate dehydrogenase, malic enzyme, mannose phosphate isomerase, nucleoside phosphorylase, octanol dehydrogenase, peptidase, 6-phosphogluconate dehydrogenase, phosphoglucomutase, and phosphoglucose isomerase (Moncrief, 1993).

Although fox squirrels occasionally follow female eastern gray squirrels in estrus, copulation is not attempted (Koprowski, 1991c; Moore, 1968). Hybridization with congeners is not known (Gurnell, 1987).

**REMARKS.** *Sciurus* is derived from the ancient Greek, *skia* meaning shadow or shade, and *oura* or tail; *niger* refers to the black coloration or the type specimen. Additional names are cat squirrel and stump-eared squirrel (Flyger and Gates, 1982).

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